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## On the characters and relationships of the Platanaceae \*

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(WITH PLATE 25)

Recent writers under the leadership of Niedenzu (1) in the Engler and Prantl *Pflanzenfamilien* have agreed in placing the Platanaceae in the Rosales between the Saxifragaceae and the Rosaceae. But as to the characters of the family, which of course form the basis of all deductions concerning its relationships, there is no agreement. This is very strikingly brought to notice by comparison of two leading floras recently published almost simultaneously. Robinson and Fernald in Gray's *New Manual* (2) state that the flowers are "destitute of calyx and corolla" while Gleason, (3) describing the Platanaceae in the *North American Flora*, attributes both calyx and corolla to the flowers.

Neither of these authors is to be held accountable for the statements in his description, for both are undoubtedly compilations from older authorities. Indeed, Robinson and Fernald's description is copied verbatim from Gray's fifth (4) and sixth editions published as long ago as 1867. But since the appearance of the *Pflanzenfamilien* in 1891, which figured and diagrammed the flowers as having both petals and sepals, almost all writers have credited the flowers with them and have described them, sometimes in considerable detail. Of these descriptions that of Sargent (5) will serve as an example. "Calyx of the staminate flower divided into 3-6 minute scale-like sepals slightly united at the base, about half as long as the 3-6 cuneiform sulcate, scarious pointed petals; stamens as many as the divisions of the calyx, opposite them, . . . ; calyx of the pistillate flower divided into 3-6, usually 4 rounded sepals much shorter than the acute petals; stamens scale-like, elongated-obovate, pilose at the apex; ovaries as many as the divisions of the calyx, superior. . . ." And in his *Silva* (6) he gives figures and floral diagrams showing these parts.

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In view of these contradictory statements it seemed desirable to undertake a study of the genus for the purpose of ascertaining the facts and of discussing its relationships. When the matter was first taken up in 1905, it was the intention to work out the whole life history of our common sycamore, *Platanus occidentalis* L. With this end in view frequent collections were made from October to August and serial sections cut after the usual methods. This intention was frustrated by a severe frost at anthesis, which so injured the flowers that only a small portion of them ripened seed. The effects of this injury were entirely internal, however, for the heads all developed alike so that it was not possible to discriminate between the good and the bad until the sections were made — too late to replace the material the same season, and other work has prevented my doing so in succeeding years. The gaps in the life history are so great on this account that it has seemed advisable to publish only the observations on the morphology of the flower, which perhaps bears more directly on the relationships of the group. I here desire to express my thanks to my colleague, Professor John H. Schaffner, for much advice and criticism.

The head consists of a cluster of flowers so much shortened that the individual pedicels are hard to distinguish. At first sight, even under a microscope, the staminate head in section looks like a single receptacle the whole surface of which is indiscriminately covered with stamens much after the fashion of a staminate cone of *Pinus*, a similarity which is heightened by the resemblance of the stamens of the two, because of the enlarged leaf-like blade of the connective (FIG. 2). Closer scrutiny of a median section (FIG. 1), however, shows narrow furrows slightly deeper than the general surface of the head, which separate the stamens into groups of one or two (as seen in the section). These furrows are the intervals between the greatly shortened and crowded pedicels which cover the head. This is made more evident by the examination of a tangential section (FIG. 4). Each peduncle, which bears three or four stamens, is surrounded by a circular scale (*sc*, FIGS. 1, 2, 4), which tapers upward into a fringe of hairs. This is so minute and insignificant that it might easily be overlooked in the abundant hair of the head; it has no vascular supply and is only two cells in thickness; it develops early and

before flowering time its cells are dead, leaving it simply a hairy fringe. Beyond these scales the staminate flowers are entirely naked until long after the stamens are completely formed. When growth is resumed after the winter, however, the receptacle, which has remained flat up to that time, begins to swell and forms bulging protuberances between the filaments (FIG. 2, *O*). In cross-section (FIG. 3) these are seen to be alternate with the stamens. They are the structures which have been called vestigial carpels.

Sections of the carpellate head (FIGS. 5-7) show an exactly similar condition. The shortened closely crowded peduncles are surrounded by vestigial sheathing bracts. The folded carpels, usually 6-9 in number, are located rather indiscriminately over the upper surface of the receptacle but with their inner open sides facing the center (FIG. 6). Beside these the only other floral parts present are three or four hairy staminodes (*s*, FIGS. 5-7), which fold over the carpels and protect them until just before anthesis. While the homology of the outgrowths from the receptacle of the staminate flower to carpels is somewhat uncertain because of their rudimentary condition, there is little doubt that these appendages of the carpellate flower are homologous with stamens. They develop before the carpels, have a strong vascular supply, and are even sometimes quadrilateral.

Such being the condition of the flowers, one turns with wonder to the accounts of those authors who give not only descriptions but figures of the petals and sepals. As has been said the account in the *Pflanzenfamilien* is the source of all the later descriptions. But this is itself a compilation from the work of Schoenland (7), from which its figures are copied. Schoenland describes the perianth very circumstantially and in considerable detail. According to him, I translate (p. 310): "The flowers are perigynous; they possess always two regular, alternating, characteristically different circles of involucreal leaves each part of which may however show considerable variation. I have no hesitation therefore in designating the outer as calyx and the inner as corolla. . . . These circles are 3-6-parted (perhaps also to 8-parted). The numerical relations may vary in one and the same inflorescence. In the staminate flowers the 4-parted condition is most frequent." He figures a tetramerous pistillate flower with sepals, petals, stami-

nodes, and carpels in regular circles, the parts of which alternate with each other. In this figure the divisions of the corolla are about half as long as the carpels—so large that they could scarcely be overlooked on examination even with a hand lens. He supplies diagrams also, showing trimerous, tetramerous, and hexamerous flowers with the parts equidistant in regular circles.

Only a few stages, however, are favorable for study. He says (p. 309): "The best time for the study of the completely developed flower is when the anthers have just begun to shed their pollen. Before this period the investigation is enormously difficult; afterwards the staminate flowers dry up and become unfavorable for investigation; likewise the pistillate flowers shed a part of their organs very quickly after anthesis. In fruit a strong growth of hair very similar to the pappus of the Compositae develops around the carpels, so that it is no wonder that even eminent botanists have stated that the perigynium of the Platanaceae is reduced to hair-like scales between the separate flowers, which represent the floral parts." But even at this favorable period he was able to find no constancy in the regular cycles he figures. On this point he says (p. 311): "In the case cited above where the different organs of the flower occur in like number the confirmation of the diagrams, empirically obtained, was more or less easy. But on account of the crowding of the flowers all possible cases of displacement, suppression, and stunting of the organs are brought about, so that in many flowers one can determine absolutely nothing with certainty regarding the spacial relations of the parts."

Schoenland did his work only a few years after the appearance of Eichler's *Blütendiagrammen*, when the influence of Eichler's school was at its height. This school had already pushed the method of studying flowers by means of the comparison of floral diagrams to great extremes. Their method had proved so useful that it was supposed that the flowers of all plants must be referable in some way or other to such regular schemes. Under the influence of this school Schoenland seems to have labored principally to verify a diagram representing the cycles which he supposed ought to be present. In this deductive method of reasoning he was prevented from checking his results by the facts because of his

supposition of a deciduous perianth and of modifications due to pressure, factors which though potent in many cases cannot be invoked to explain the flowers of *Platanus*.

Moreover, because of the hairiness and the early lignification of the inflorescence the sycamore is an exceedingly difficult object to handle even by the best methods of modern technique, which had not been invented at the time of Schoenland's work. He himself recognized very clearly the insufficiency of his methods, concerning which he says (p. 313): "A complete isolation of the individual young flowers is possible and was accomplished by me in different ways; but the advantages obtained thereby are very doubtful, since, because of the density of the inflorescence, parts of the preparations are easily torn off, which naturally introduces numerous errors.

"I have preferred therefore for the most part to cut thin sections from heads hardened in alcohol, and to observe them in glycerine by reflected and transmitted light. The thick pubescence of the bud-scales and of the sepals is extremely disturbing, so that for the most part one can determine in this way nothing certain regarding the sepals or the petals which they cover, especially since there occur, irregularly distributed between the individual flowers, rather long hairs which are entirely distinct from the pappus-like hairs of the fruit. In the staminate or apparently perfect flowers this method is of no service, since here the thick pubescence of the anthers or staminodes makes every observation impossible. In these I was limited to longitudinal sections of the flowers, and although I am aware that one can use results which are obtained in such a way only very cautiously, on account of the impossibility of orienting the sections satisfactorily, yet I believe that I have reached correct conclusions from them, since they are in perfect accord with the facts otherwise determined." We must admire the perseverance of a man who was willing to attempt scientific work under such difficulties but we cannot give much weight to his results.

It is apparently safe to assume that the inflorescence of *Platanus* has attained its present very compact condition by the shortening of the pedicels of the individual flowers. To what extent this shortening has involved loss of floral parts is a matter

of conjecture. Such shortening might be expected to favor the development of perigyny but the flowers are clearly hypogynous (FIGS. 1, 2, 5) and have no perigynous disc as Schoenland maintains. The presence of staminodes and of rudimentary carpels seems to indicate clearly that the flowers were originally perfect. The homology of the scale encircling the pedicel is somewhat doubtful. It may be the vestige of the calyx. But its form suggests strongly the sheathing base of a foliage leaf. If it is to be compared with a leaf it would represent a vestigial bract surrounding the pedicel as the bases of the leaves surround the buds in their axils. But it is so much reduced that it is not possible in my judgment to determine with certainty what it represents.

Whether this represents a bract or a calyx, it is clear that *Platanus* is apetalous and that it should be removed from the Rosales and placed among the Apetalae. In this group the place of the Platanales is probably to be found next the Urticales. This position they originally held on account of their obvious resemblances to some of the Urticales. There seem to be in this case no characters of the life history which are more significant than those general similarities that every observer recognizes, namely: the tendency toward the aggregation of the flowers into spherical heads by the shortening of the pedicels, which has been carried to its culmination in *Platanus* and such genera of the Urticales as *Artocarpus* and *Toxylon*, and the development of sheathing stipules completely encircling the stem and covering the bud as in *Artocarpus* and *Ficus*. Between these genera and *Platanus* there is of course a gap so wide as to be of ordinal rank, and yet these similarities may indicate the approximate place of the Platanales among the orders of the Apetalae and save it from complete isolation.

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#### Explanation of plate 25

The figures are camera drawings of microtome sections. *c*, carpel; *o*, outgrowth from receptacle of staminate flower = vestigial carpel; *s*, staminode; *sc*, encircling scale; *st*, stamen.

FIG. 1. Portion of a median section of a staminate head, showing one flower with parts of two others at the sides,  $\times 65$ . October 3.

FIG. 2. Longitudinal section of a staminate flower, showing outgrowths from the receptacle, which are doubtfully homologized with carpels,  $\times 25$ . April 25.

FIG. 3. Cross section through the filaments of a flower of the same age as fig. 2,  $\times 65$ .

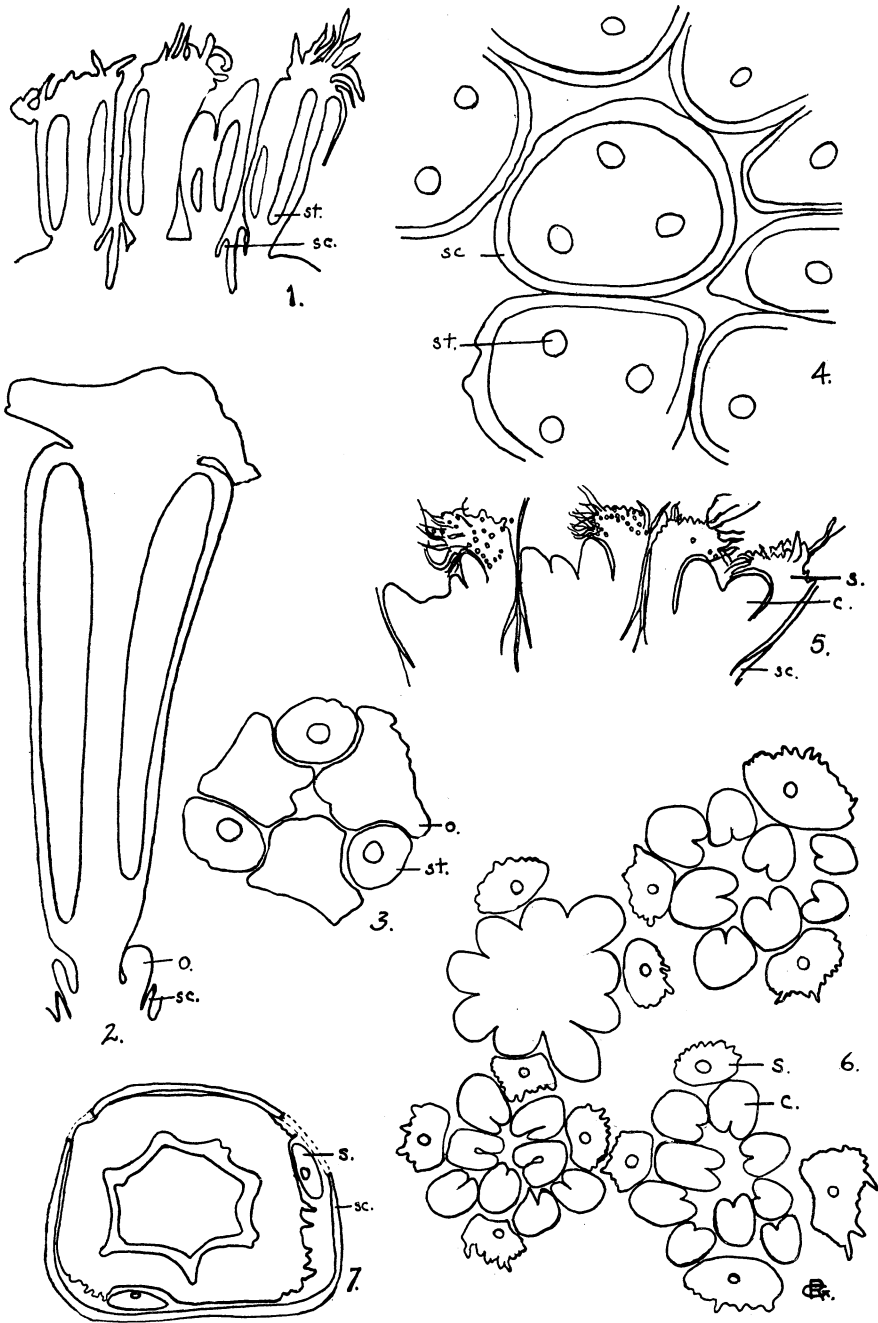
FIG. 4. Tangential section through the pedicels of a staminate inflorescence of same age as figs. 2 and 3,  $\times 65$ .

FIG. 5. Longitudinal section of a group of carpellate flowers,  $\times 25$ . January 15.

FIG. 6. Tangential section of a carpellate head,  $\times 65$ . April 18.

FIG. 7. Similar section at the level of the encircling scale,  $\times 65$ . April 18.





GRIGGS, CHARACTERS OF THE PLATANACEAE